Leptostroma on pine needles

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Received July 23, 1979

MINTER, D. W. 1980. *Leptostroma* on pine needles. Can. J. Bot. **58**: 906–917.

The eight species and one variety of *Leptostroma* Fr. ex Fr. hitherto described on needles of *Pinus* L. are examined and where possible related to anamorphs of species of *Lophodermium* Chev. and *Meloderma* Darker. Three groups of these conidiomata can be distinguished based on the depth to which they are embedded in the needles and how they open. Within each group conidiomata of individual species are often hard to identify. Each group is keyed out and illustrated. ***Lophodermium molitoris*** sp.nov. and *Lophodermium baculiferum* Mayr with their respective *Leptostroma* stages are described and illustrated and *L. baculiferum* and *Leptostroma strobicola* Hilitz. are neotypified. Three species of *Leptostroma* which cannot be related to anamorphs of *Lophodermium* and *Meloderma* are excluded from *Leptostroma*.

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Les huit espèces et une variété de *Leptostroma* Fr. ex Fr. déjà décrites sur les aiguilles de *Pinus* L. sont examinées et, autant que possible, reliées aux anamorphes d'espèces de *Lophodermium* Chev. et *Meloderma* Darker. On peut distinguer trois groupes de ces "conidiomata" d'après la profondeur à laquelle ils sont enfouis dans les aiguilles et d'après leur façon de s'ouvrir. A l'intérieur de chaque groupe, les "conidiomata" d'espèces individuelles sont souvent difficiles à identifier. Chaque groupe est distingué par une clef d'identification et illustré. ***Lophodermium molitoris*** sp.nov. et *Lophodermium baculiferum* Mayr ainsi que leurs stades *Leptostroma* respectifs sont décrits et illustrés; *L. baculiferum* et *Leptostroma strobicola* Hilitz. sont néotypifiés. Trois espèces de *Leptostroma* qui ne peuvent être reliées à des anamorphes de *Lophodermium* et *Meloderma* sont exclues du genre *Leptostroma*.

[Traduit par le journal]

Species of *Lophodermium* Chev. (Ascomycetes, Phacidiales) fruiting on needles of *Pinus* L. produce as anamorphs small stromatic conidiomata immersed in the needles and opening by ostioles and tears in the surface. These have usually been referred to the form genus *Leptostroma* Fr. ex Fr. Recent taxonomic work has provided detailed descriptions of the teleomorphs of these species (Minter *et al.* 1978; Minter and Millar 1978*a*, 1978*b*) but except for the works of Darker (1932) and Jones (1935) the anamorphs have never been illustrated or described in detail. In this study validly published taxa of *Leptostroma* described as occurring on pine needles were examined and where possible related to the anamorphs of species of *Lophodermium* and the closely related genus *Meloderma* Darker. Where an association with a teleomorph is suggested, conidiomata and ascocarps were seen on the same region of needle, and in species producing zone lines, between the same pair of zone lines. These taxa fell into three clearly defined groups, each containing anamorphs of more than one species of *Lophodermium* or *Meloderma*. Within each group separation of the anamorphs, if possible, was by careful measurement of a great number of conidia.

The most useful characteristics for distinguishing the three groups are depth to which the conidiomata are immersed in the needles and the manner in which they open. In vertical section one group produces conidiomata immersed below the needle cuticle, while those of the other two groups are subepidermal. Conidiomata of the subcuticular group split open with irregular tears in the surface, and when ostioles occur they are scattered in the upper wall. Of the subepidermal groups, one produces one to several small ostioles more or less in the centre of the upper wall and infrequently opens by a longitudinal split at one side of the conidioma, while the other group always opens by such a split and ostioles when produced are located along this split line. Each group is illustrated diagrammatically in Fig. 1.

In addition to the features mentioned above, some conidiomata have been observed which contain among the conidiogenous cells vertical hyphae which are distinctly longer and broader than the conidiogenous cells, though roughly the same shape, clustered in a group below an ostiole or scattered among the conidiogenous cells (Fig. 2). These hyphae, whose function is not known, were first noticed and illustrated by Jones (1935), who suggested that they might have a sexual role as trichogynes. Since they are rather infrequently en-

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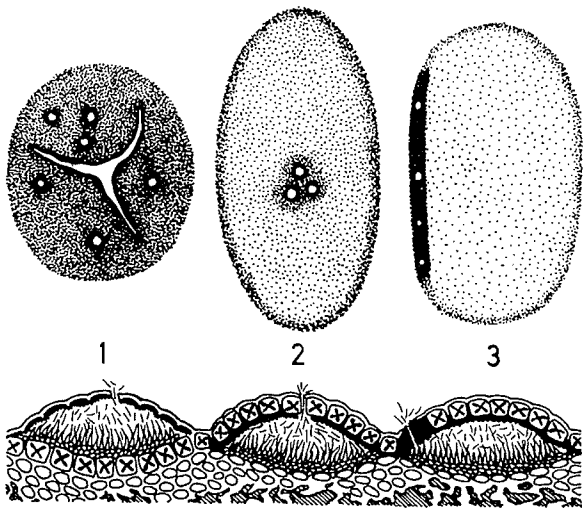


FIG. 1. Conidiomata of each group viewed from above and in vertical section (diagrammatic).

countered, they are omitted from the descriptions below.

Leptostroma Fr. ex Fr., Syst. Mycol. 2: 597 (1823)

Conidiomata eustromatic, scattered, immersed in the abaxial and adaxial or radial surfaces of needles, externally appearing as circular to elongated elliptical blisters, level with or slightly raised from the needle surface, concolorous with the needle, or grey to black or brown, smooth or wrinkled, with or without ostioles, most species also opening by one or more tears in the surface; coalescing rarely to frequently to form bilocular or multilocular conidiomata. Conidiomata are composed of an upper and a lower wall. The upper wall when examined from above is composed of more or less brown cells with more or less blackened walls, 2–8 μm diameter, forming a textura angularis which extends over some, most, or all of the conidioma. In some species the texture changes abruptly from angularis to aliform (Tehon 1935) near the margin of the conidioma. Ostioles, when present, are circular pores through this upper wall, the cell walls of which may be noticeably more blackened near any ostioles or splits. Examined in vertical section, the conidiomata are located beneath either the cuticle or the epidermis of the needle, which forms a cover. The upper wall can be seen as a blackened layer, one cell thick, adjacent to this cover. The lower wall, adjacent to and above the needle epidermis or hypodermis (depending on the depth of embedding of the conidioma), is a layer of hyaline, rarely pale brown, thin-walled cells, 2–6 μm diameter, forming a textura angularis 6–12 μm deep. In some species

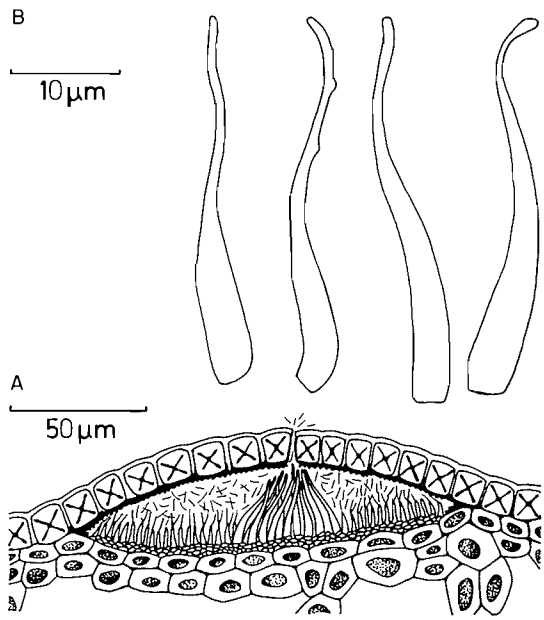


FIG. 2. Trichogynes. (A) Clustered below an ostiole (vertical section of *Leptostroma pinorum* var. *cembrae*). (B) Detail of individual trichogynes.

the walls of the cells nearer the epidermis or hypodermis are more or less blackened. Conidiophores absent. Conidiogenous cells holoblastic, sympodial to synchronous, indeterminate, discrete, subcylindrical to tapering, hyaline, thin walled smooth. Conidia hyaline, aseptate, thin walled smooth, more or less rod shaped, with or without small droplets, emerging from the ostioles or splits of the conidioma in gummy masses. Zone lines formed across the needle in association with conidiomata of some species.

Conidiogenous cells and conidia of *Leptostroma pinorum* Sacc. are illustrated in Fig. 3. Those of other species are very similar in shape and differ, often only slightly, in size.

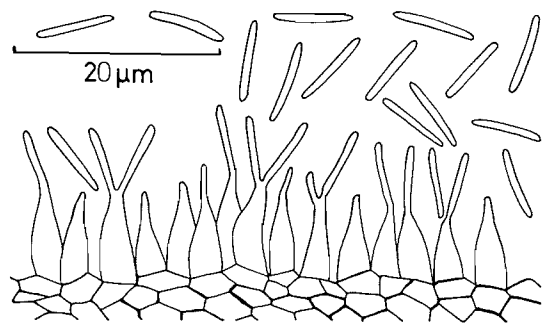


FIG. 3. Conidiogenous cells and conidia of *Leptostroma pinorum*.

KEY TO *Leptostroma* SPECIES ON PINE NEEDLES

1. Conidiomata subcuticular (group 1) 2
   Conidiomata subepidermal 4

2. On primary (seedling) needles ..... *Leptostroma austriacum*
   On secondary (mature plant) needles 3

3. Ostioles present, conidiomata usually associated with many black zone lines formed across the needle ..... *Leptostroma* stages of *Lophodermium nitens* and *Lophodermium molitoris*
   Ostioles absent, conidiomata never associated with black zone lines formed across the needle *Leptostroma strobicola*

4. Ostioles present in centre of upper wall (group 2) ..... all *Leptostroma* species of group 2
   Ostioles (if present) in split line (group 3) 5

5. Conidiomata usually concolorous or only slightly darker than the needle surface ..... *Leptostroma* stages of *Lophodermium pinastri* and *Lophodermium pini-excelsae*
   Conidiomata usually dark grey to blackish ..... *Leptostroma decipiens*

Group 1

Leptostroma stage of *Lophodermium nitens* Darker, J. Arnold Arbor. Harv. Univ. 1: 74 (1932) (Figs. 4–6)

Conidiomata externally appearing as more or less circular blisters, 50–400 μm diameter, slightly raised from the needle surface, pale brown to black and shiny, smooth or wrinkled, with a well-defined margin, with one to several inconspicuous ostioles, also opening by one or more irregular tears in the surface; infrequently coalescing to form bilocular or multilocular conidiomata. The upper wall of the conidioma, when examined from above, extends over the whole of the conidioma, with ostioles seen as circular pores, 3–10 μm diameter, occurring scattered in the upper wall, the cell walls of which may be noticeably more blackened near the ostioles and splits. The conidiomata examined in vertical section are subcuticular and those cells of the lower wall which are nearest the needle epidermis have blackened walls and may be slightly brown. Conidiogenous cells 8–12 μm × 2.5–4 μm. Conidia 6–9 μm × 1 μm. Zone lines black, thin, usually frequent.

SPECIMENS EXAMINED: On *Pinus strobus*, Bear Island, Lake Timagami, Ontario, Canada, 27 May 1924, G. D. Darker (cotype of *Lophodermium nitens*), K; on *P. strobus*, Shelburne, New Hampshire, May 1900, W. G. Farlow (Reliquiae Farlowianae 50) (as *Lophodermium pinastri*), K; on *P. monticola*, Priest River, Idaho, 3 August 1915, J. R. Weir (as *L. pinastri*), K; on *P. lambertiana*, Calaveras State Park, Calaveras Co., California, U.S.A., 24 May 1959, Lee Bonar, K; on *P. lambertiana*, Sagehen Creek Biological Station, Nevada County, California, U.S.A., 5 August 1965, Lee Bonar, IMI 142256; on *P. lambertiana*, Yosemite National Park, California, U.S.A., 24 June 1933, Lee Bonar, IMI 23113.

Leptostroma stage of *Lophodermium molitoris* sp.nov.

Lophodermium molitoris described below differs from *L. nitens* only in minor details of the ascocarp structure. The two species are closely related and their *Leptostroma* stages are indistinguishable.

Lophodermium molitoris sp.nov. (Figs. 7–9)

A *Lophodermio nitenti* differt quod in rima habet cellulas labiales. Ab aliis *Lophodermii* speciebus quae acus incolent pini differt quod conidiomata et ascocarpos habet subcuticularia.

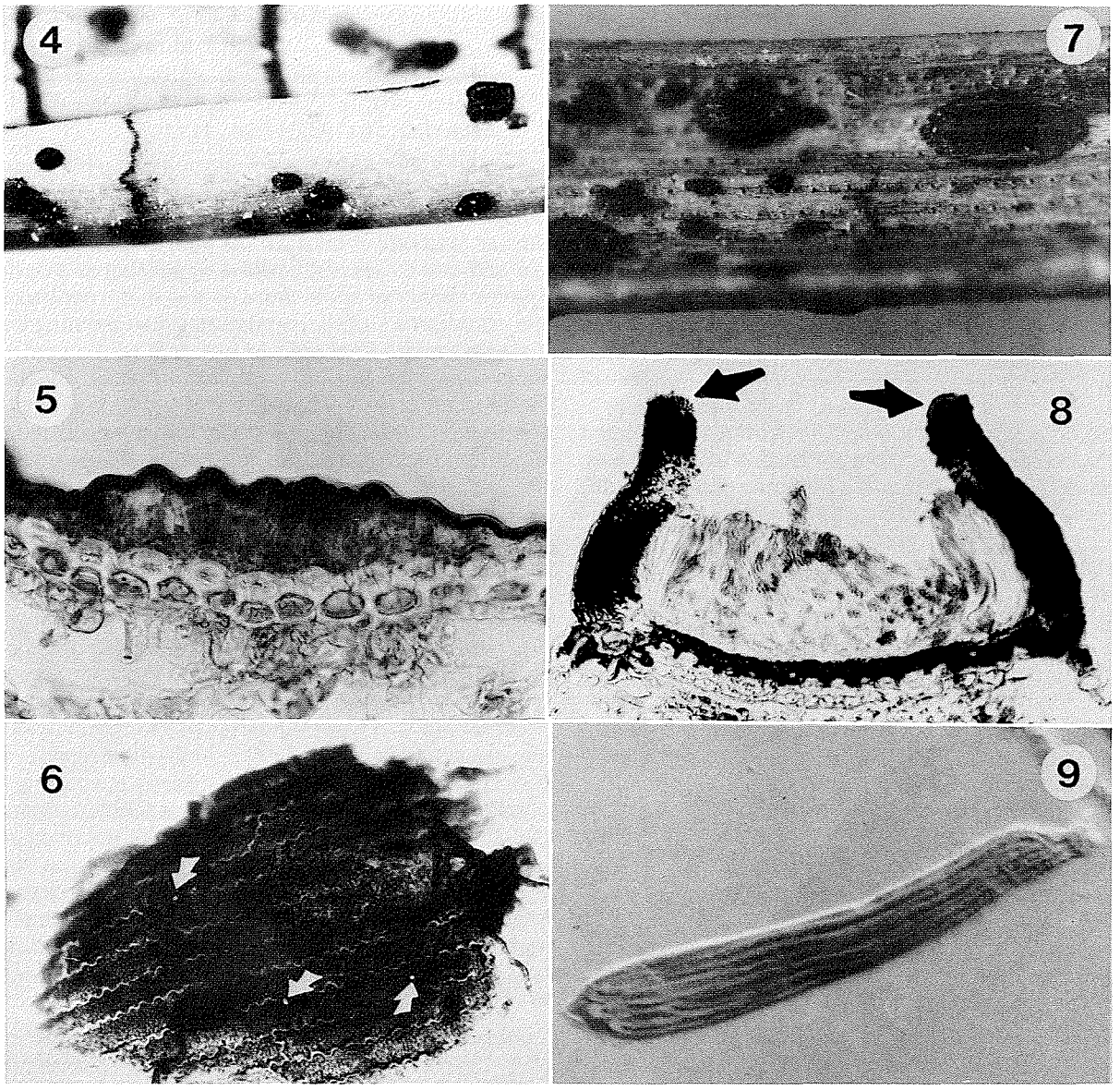
Ascocarpis in acubus amphigenis, 500–1000 μm long., ellipticis, nigris licet sint statu udo vel sicco, subcuticularibus, rima quibusque aperientibus longitudinali quae cellulis labialibus hyalinis induta est. Paraphysibus filiformibus, simplicibus, hyalinis, rectis vel flexuosis, apice nil inflatis, ascis aequilongis. Ascis cylindricis, octosporis, 90–130 μm × 10–14 μm. Ascosporis filiformibus, aseptatis, hyalinis, levibus, in muco involutis, 80–120 μm × 2 μm, fasciculatis et saepe versus asci apicem spirales ostendentibus convolutas. Conidiomatibus plus minusve circularibus, 50–400 μm diam., fulvis vel nigris, nitidis, ostiolatis, subcuticularibus. Cellulis conidiogenis holoblasticis, sympodialibus, subcylindricis, 8–12 μm × 2.5–4 μm. Conidiis bacillaribus, aseptatis, hyalinis, levibus, 6–9 μm × 1 μm. Lineis zonalibus tenuibus, nigris, transversalibus, acus transeuntibus, frequentibus, fructificationes comitantibus.

HOLOTYPUS: In foliis *Pini banksianae*, Macdowall, Sask., Canada, 23 July 1935, R. C. Russell, IMI 23110.

SPECIMENS EXAMINED: On *Pinus banksiana*, Macdowall, Sask., Canada, 29 June 1938, R. C. Russell, IMI 23115; on *P. banksiana*, Diamond Lake, Timagami, Ont., Canada, 30 August 1935, R. F. Cain, IMI 73332.

The specific epithet derives from the Latin word for a miller, in honour of the forest pathologist C. S. Millar.

Lophodermium molitoris is very similar to *L. nitens*. Both species have similar anamorphs, thin black zone lines, textura prismatica in the developing ascocarps, as described by Gordon (1968), and subcuticular ascocarps. No other species of *Lophodermium* with subcuticular ascocarps has been described on needles of pine, although several



FIGS. 4–6. *Leptostroma* stage of *Lophodermium nitens*. Fig. 4. Conidioma and zone lines surface view. × 30. Fig. 5. Conidioma vertical section. × 380. Fig. 6. Conidioma surface view under transmitted light showing upper wall texture and ostioles (arrowed). × 220. FIGS. 7–9. *Lophodermium molitoris*. FIG. 7. Ascocarps and conidiomata surface view. × 30. FIG. 8. Ascocarp vertical section, note lip cells (arrowed). × 160. FIG. 9. Ascus. × 720.

species produce ascocarps which are partly subcuticular and partly subepidermal (Minter *et al.* 1978). The position of the ascocarp in needle tissues is a very reliable specific characteristic for *Lophodermium* species on pine (Minter *et al.* 1978).

Lophodermium molitoris differs from *L. nitens* in having lip cells lining the split. Lip cells are present in most species of *Lophodermium* on pine needles, though they tend to be lost in old ascocarps which have finished releasing their ascospores. They are such a constant feature of mature ascocarps of these species that their presence in *L. molitoris* is considered sufficient justification for describing a new species. Ascocarps of *L. nitens* never produce lip cells but open characteristically with a tearing of the blackened upper wall.

Leptostroma strobicola Hilitz., Věd. Spisy Česk. Akad. Zeměd. 3: 149 (1929). Anamorph of *Meloderma desmazierii* (Duby) Darker, Can. J. Bot. 45: 1429 (1967)

Differs in the following ways from *Leptostroma*

stage of *L. nitens*: conidiomata infrequent, immersed in the abaxial more often than the adaxial or radial surfaces of needles, with no ostioles, the lower wall with no observable blackening of the cell walls. Conidia 5–8 μm × 1 μm. Zone lines absent.

SPECIMEN EXAMINED: On *Pinus strobus*, London, Ontario, Canada, 18–25 September 1923, J. Dearness, IMI 19818.

Hilitzer's original description cited no specimen, but defined *L. strobicola* as the anamorph of *Hypoderma* (*Meloderma*) *desmazierii*. The specimen cited above agrees closely with his description and is selected as neotype. *Leptostroma strobicola* is very similar to the *Leptostroma* stages of *Lophodermium nitens* and *L. molitoris*, but is produced in far smaller numbers without associated black zone lines. Reliable separation of these three anamorphs by light microscope morphological differences is not possible.

Leptostroma austriacum Oud., Versl. Meded. Akad. Wetenschappen, Amsterdam, p. 208 (1904). Sacc. Syll. Fung. 18: 427 (1906) (Fig. 10)

Differs in the following ways from *Leptostroma* stage of *L. nitens*: conidiomata on primary (seedling) needles, more or less elliptical, frequently coalescing to form bilocular or multilocular conidiomata. Zone lines absent.

SPECIMEN EXAMINED: On *Pinus austriaca*, Schoorl, Amsterdam, Netherlands, 12 June 1904, J. Ritzema Bos, type, L.

Oudeman's original description stated that the fungus was found fruiting on needles of young plants of *Pinus austriaca* killed by a *Fusarium* root infection. Examination of the type material revealed that the *Leptostroma* was occurring on the primary needles (needles produced singly, not in bundles, in the first 2 years of the plant's life). Nothing is known of the appearance of other species of *Leptostroma* on primary needles and it is possible that the different structure of these needles may affect the depth to which the conidiomata are embedded. *Leptostroma austriacum* is retained as a name for subcuticular conidiomata on primary needles until the behaviour of other *Leptostroma* species on this substrate is known.

Group 2

Leptostroma pinorum Sacc., Michelia, 2: 632 (1882). Anamorph of *Lophodermium conigenum* Hilitz., Věd. Spisy Česk. Akad. Zeměd. 3: 76 (1929) (Figs. 11–14)

Conidiomata appearing externally as elongated elliptical blisters, 300–550 μm × 200–280 μm, concolorous with the needle or greyish and slightly darker, smooth, with a darker poorly defined margin and one to several ostioles appearing as a dark spot or cluster of spots more or less in the centre of the conidioma surface, sometimes also opening by a single longitudinal split to one side of the conidioma along the line of weakness afforded by the stomata or between two rows of epidermal cells; frequently coalescing to form bilocular or multilocular conidiomata, the coalescing being mostly longitudinal, rarely lateral, multilocular conidiomata being up to about 1 cm long. The upper wall of the conidioma, when examined from above, may extend over the whole of the conidioma, but is usually limited to an area within a radius of about 30 μm from the nearest ostiole and to a region about 20 μm wide marking the edge of the conidioma. Blackening is heavier near the stomata and split when splitting occurs. Ostioles can be seen as circular pores about 8–15 μm diameter in the upper wall, above each of which careful examination reveals a thin split about 10 μm × 4 μm either between two needle epidermal cells or through a single epidermal cell and in both cases also through the overlying needle cuticle. Examined in vertical section the conidiomata are subepidermal and the cells of the lower wall are not or only slightly blackened. Conidiogenous cells 5–10 μm × 2–4 μm. Conidia 4.5–9 μm × 1 μm. Zone lines brown, diffuse, infrequent or absent.

SPECIMENS EXAMINED: On *Pinus* sp., Brionne, Malbranche, France, Herb. P. A. Saccardo, holotype, PAD; on *P. pinaster*, Azores, 27 March 1975, R. W. G. Dennis, K; on *P. pinaster*, Praia do Guincho, Estramadura, Portugal, 2 April 1979, B. L. K. Brady, IMI 238667; on *P. pinaster*, Tarland, Aberdeenshire, Scotland, October 1976, D. W. Minter, IMI 231787; on *P. sylvestris*, Tarland, Aberdeenshire, Scotland, 17 February 1975, D. W. Minter, IMI 231777; numerous other collections on *P. sylvestris* from Great Britain examined.

Conidiomata of *L. pinorum* on *P. sylvestris* contain conidia distinctly shorter than those on *P.*

FIG. 10. *Leptostroma austriacum*, surface view. × 40. FIGS. 11–14. *Leptostroma pinorum*. FIG. 11. Conidioma surface view. × 30. Fig. 12. Conidioma vertical section. × 260. Fig. 13. Conidioma surface view under transmitted light showing detail of ostiole, note also textura angularis of upper wall in a limited area around the ostiole. × 580. Fig. 14. As Fig. 13, but focussed to show the split between epidermal cells above the ostiole. × 600. FIG. 15. *Leptostroma pinorum* var. *cembrae* surface view. × 30. FIG. 16. *Leptostroma durissimum* surface view, note dark split lines at the sides of some conidiomata. × 30. FIG. 17. *Leptostroma* stage of *Lophodermium pinastri*.

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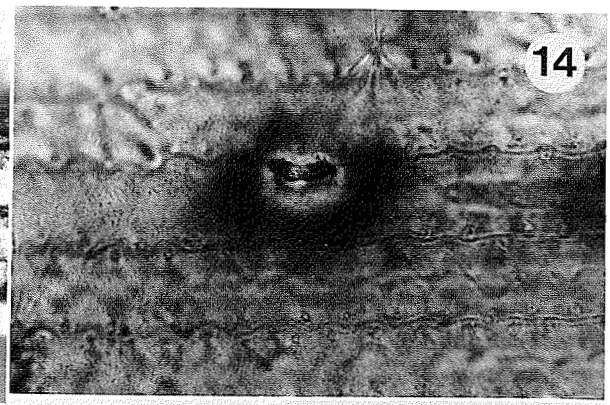
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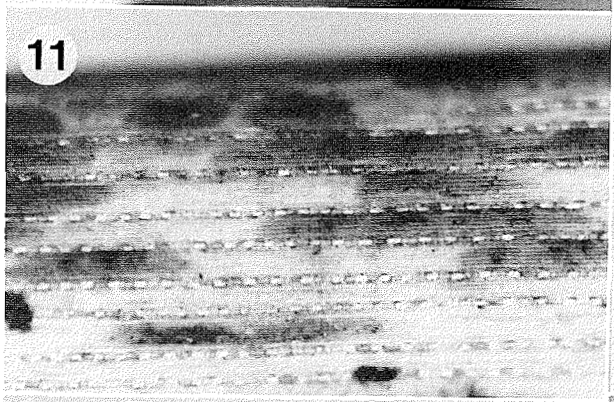
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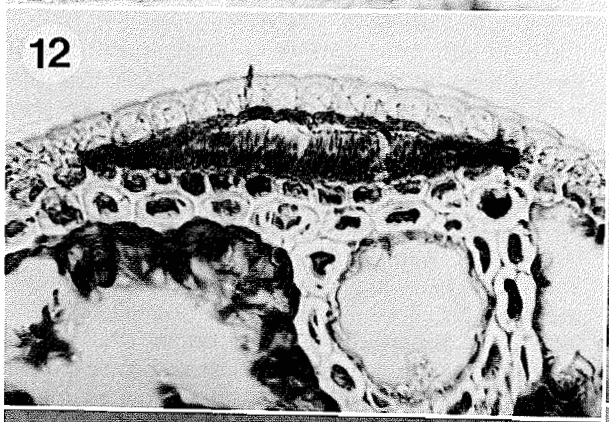
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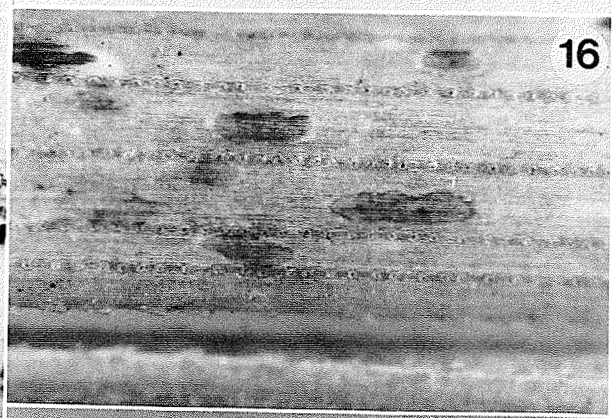
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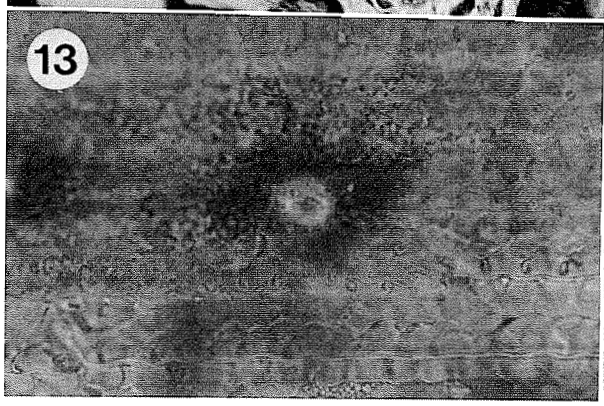
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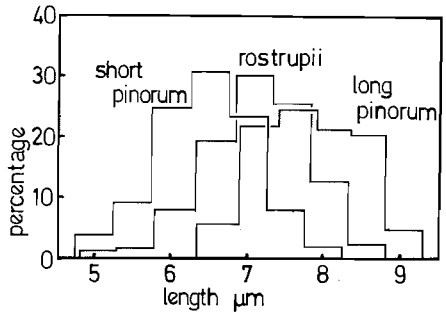


FIG. 18. Histogram comparing conidia lengths of *Leptostroma rostrupii* (n = 411) and "long" (n = 168) and "short" (n = 282) *L. pinorum*.

pinaster (Fig. 18, marked "short pinorum" and "long pinorum" respectively), although the teleomorphs with which each is associated are at present indistinguishable.

Leptostroma pinorum var. ***cembrae*** (Bubák & Kabát) comb.nov. Basionym: *Leptostroma pinastri* var. *cembrae* Bubák & Kabát, Ann. Mycol. 13: 111 (1915) (Fig. 15)

Differs from *L. pinorum* by having less elongated conidiomata coalescing less frequently, although associated with an indistinguishable teleomorph. Conidia are the same length as in "long pinorum." Known only on *P. cembra*.

SPECIMENS EXAMINED: On *P. cembra*, Monte Ciampedie, Fassathale, South Tyrol, Austria, 20 August 1913, J. E. Kabát, isotype, K; on *P. cembra*, Tyrol, Austria, August 1872 (as *Lophodermium pinastri*), Rehm, Ascomyceten 127, K.

Leptostroma rostrupii nom. nov. for *Depazea linearis* Rostr., Tidsskr. Skogbr. 6: 260 (1883). Non *Leptostroma lineare* Lev. Anamorph of *Lophodermium seditiosum* Minter, Staley & Millar, Trans. Br. Mycol. Soc. 71: 300 (1978)

Differs slightly in conidia lengths from *L. pinorum* (Fig. 18).

SPECIMENS EXAMINED: On *P. sylvestris* (eight collections), on *P. montana* (two collections), on *P. austriaca* (five collections), Herb. E. Rostrup, C; on *P. sylvestris*, Gray's Harbor Co., Washington, U.S.A., September 1973, C. S. Millar & J. M. Staley, holotype of *Lophodermium seditiosum*, IMI 225142; numerous other collections on *P. sylvestris* from Great Britain examined.

Rostrup's specimens and original description make it clear that his species is the anamorph of *Lophodermium seditiosum*.

Leptostroma durissimum Cooke, Grevillea, 7: 32 (1878). Anamorph of *Lophodermium australe* Dearn., Mycologia, 18: 242–243 (1926) (Fig. 16)

Differs slightly from *L. pinorum* and *L. rostrupii* by opening more frequently with a longitudinal split at the side of the conidioma. Conidia lengths are indistinguishable from "long pinorum." *Leptostroma durissimum* is associated with *Lophodermium australe* in the type material.

SPECIMENS EXAMINED: On *Pinus* sp., Aiken, South Carolina, U.S.A., Herb. M. C. Cooke, holotype, K; on *P. taeda*, Marion, South Carolina, U.S.A., 3 April 1926, G. G. Hedgecock, K; on *P. taeda*, Pittsboro, North Carolina, U.S.A., 14 December 1927, J. Dearness, IMI 92455; on *P. caribaea*, Mountain Pine Ridge, Forest Reserve, Belize, 29 July 1974, J. Hudson, IMI 187034; on *P. caribaea*, Rio Negro, Brazil, 1971, L. C. May, IMI 156989; on *P. caribaea*, Australia, 5 October 1973, M. M. Clay, IMI 179652; numerous other specimens on subtropical pines (*P. elliottii*, *P. kesiya*, *P. palustris*, *P. patula*) examined.

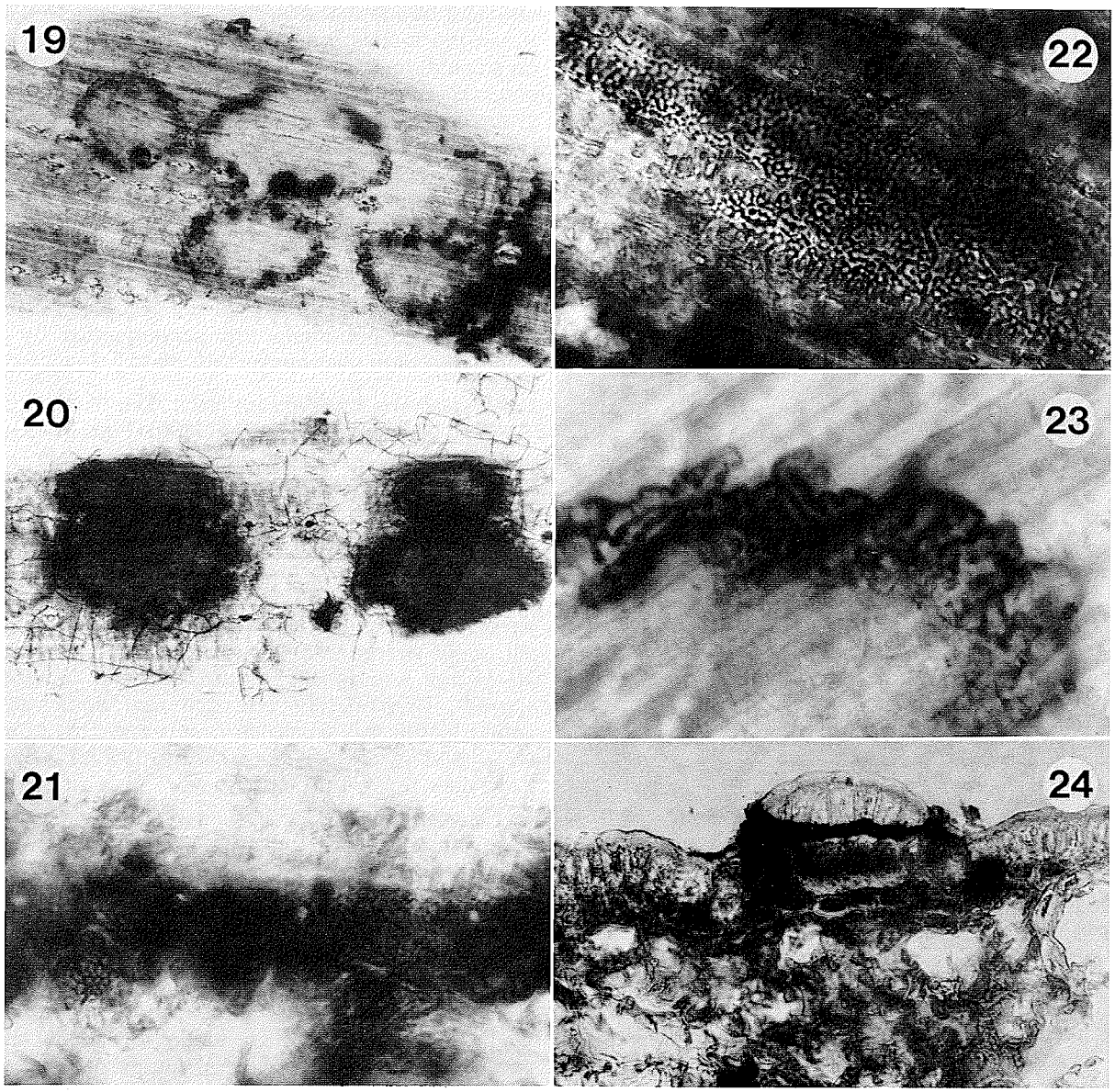
The similarity of their *Leptostroma* stages provides evidence that *Lophodermium australe* and *L. conigenum* intergrade. Reliable separation of the species in this group is possible only by reference to their teleomorphs (Minter and Millar 1978*a*) or in some cases by measurement of a great number of conidia.

Group 3

Leptostroma stage of *Lophodermium pinastri* (Schrad. ex Hook.) Chev., Flora Env. Paris, 1: 436 (1826) (Figs. 17, 19–24)

Conidiomata externally appearing as elliptical to elongated elliptical blisters, 200–450 µm × 150–250 µm, concolorous or greyish and slightly darker than the needle, smooth, with a darker often well defined margin, with or without ostioles, opening by a single longitudinal split to one side of the conidioma along the line of weakness afforded by the stomata, or between two rows of epidermal cells, ostioles when present being found in the blackened wall lining this split; occasionally coalescing to form bilocular, less frequently multilocular conidiomata, the coalescing being lateral or longitudinal. The upper wall of the conidioma, when examined from above, extends over the whole conidioma but is often poorly blackened and hard to see. Near the margin it changes rapidly in texture to aliform tissue, which is often however poorly developed, and may be absent. Blackening is heavier near the stomata and split and ostioles may be seen as circular pores 8–15 µm diameter in the blackened wall lining the split. Examined in vertical section the conidiomata are subepidermal and the cells of the lower wall are not or only slightly blackened. Conidiogenous cells 5–10 µm × 2–5 µm. Conidia 4.5–6.25 µm × 1 µm. Zone lines black, thin, frequent.

SPECIMENS EXAMINED: On *P. sylvestris*, Mougeot & Nestler No. 76, isolectotype of *Lophodermium pinastri*, K; on *P. sylvestris*, Skiary, Kinlochourn, Wester Ross, Scotland, 26 March



FIGS. 19–24. *Leptostroma* stage of *Lophodermium pinastri*. Fig. 19. Conidioma surface view under transmitted light. Conidiomata with poorly developed upper walls. × 80. Fig. 20. As Fig. 19, but conidiomata with well-developed upper walls. × 80. Fig. 21. Conidioma surface view under transmitted light. Details of ostioles occurring along split line. × 500. Fig. 22. As Fig. 21, but detail of upper wall texture. × 550. Fig. 23. As Fig. 21, but detail of upper wall edge aliform tissue. × 550. Fig. 24. Conidioma vertical section. × 200.

1976, D. W. Minter, IMI 238368; on *P. sylvestris*, Glenetive, Argyllshire, Scotland, February 1977, D. W. Minter, IMI 231807; numerous other collections on many different species of pine examined.

Leptostroma stage of *Lophodermium pini-excelsae* Ahmad, Sydowia Ann. Mycol. 8: 172–173 (1954)

Differs in conidia lengths from *Leptostroma* stage of *Lophodermium pinastri* (Fig. 25) and in having fewer thin black zone lines.

SPECIMEN EXAMINED: On *P. sylvestris*, Deskins Farm, Oregon, U.S.A., 16 September 1973, C. S. Millar, IMI 225067.

Conidiomata seem to be formed rarely when this species occurs on five-needle (haploxylon) pines.

Leptostroma decipiens Petr., Ann. Mycol. 20: 214 (1922) (Figs. 26–30)

Conidiomata externally appearing as broadly to elongated elliptical blisters, grey to black with a

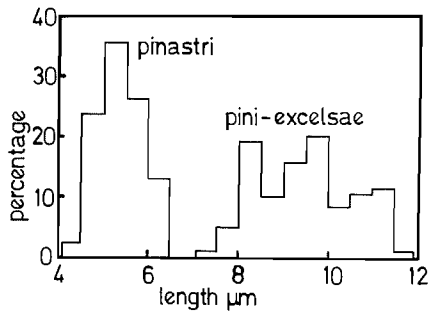


FIG. 25. Histogram comparing conidia lengths of *Leptostroma* stages of *Lophodermium pinastri* (n = 179) and *L. pini-excelsae* (n = 108).

poorly defined margin, smooth, with one to several inconspicuous ostioles in groups near the stomata which occur above the conidioma; splits not observed; usually coalescing to form bilocular or more often multilocular conidiomata, the coalescing being mostly lateral but also frequently longitudinal, giving rise to multilocular conidiomata, 200–700 µm × 150–400 µm. The upper wall of the conidioma when examined from above extends over the whole conidioma, blackening being heavier near the stomata, the texture changing rapidly near the margin which is covered by a zone 15–30 µm wide of aliform mycelium. Ostioles can be seen as circular pores 8–15 µm diameter in the upper wall, located below the cuticular covering around the stomata. Examined in vertical section the conidiomata are subepidermal (occasionally a single epidermal cell may be cast down) and the cells of the lower wall are not or only slightly blackened. Conidiogenous cells 8–12 µm × 2.5–4 µm. Conidia 9–15 µm × 1 µm. Zone lines black, thin, infrequent.

SPECIMENS EXAMINED: On *P. ponderosa*, Idaho City, Idaho, U.S.A., 21 June 1917, L. M. Benkow & J. R. Weir, Reliquiae Petrakianae 187, IMI 228857; on *P. jeffreyi*, Lassen National Forest, Lassen County, California, U.S.A., 15 August 1965, Lee Bonar, IMI 142151; on *P. jeffreyi*, Smith River, Gasquet, California, U.S.A., May 1933, H. E. Parks, IMI 23101; on *P. jeffreyi*, Gasquet, California, U.S.A., June 1933, H. E. Parks (as *Lophodermium pinicolum*), K; on *P. ponderosa*, Siskyou County, California, U.S.A., 6 July 1903, E. B. Copeland (as *Lophodermium pinastri*), Pacific Slope Fungi 3583, K.

This species was recently redescribed by Thyr and Shaw (1964), who pointed out that Petrak had inaccurately described the conidiomata as subcuticular and that Saccardo's (1920) description of *Actinothyrium marginatum* Sacc. was based partly on a conidioma of *L. decipiens*. *Leptostroma decipiens* is distinguished from other species in this group by its markedly darker conidiomata which regularly coalesce to form complex conidiomata and by the characteristic arrangement of the ostioles around the needle stomata. The conidia lengths are greater than those of the other species in this group, although they overlap with those of *Leptostroma* stage of *Lophodermium pini-excelsae*. In all but the first of the specimens cited above the conidiomata are accompanied by a *Lophodermium* teleomorph described below.

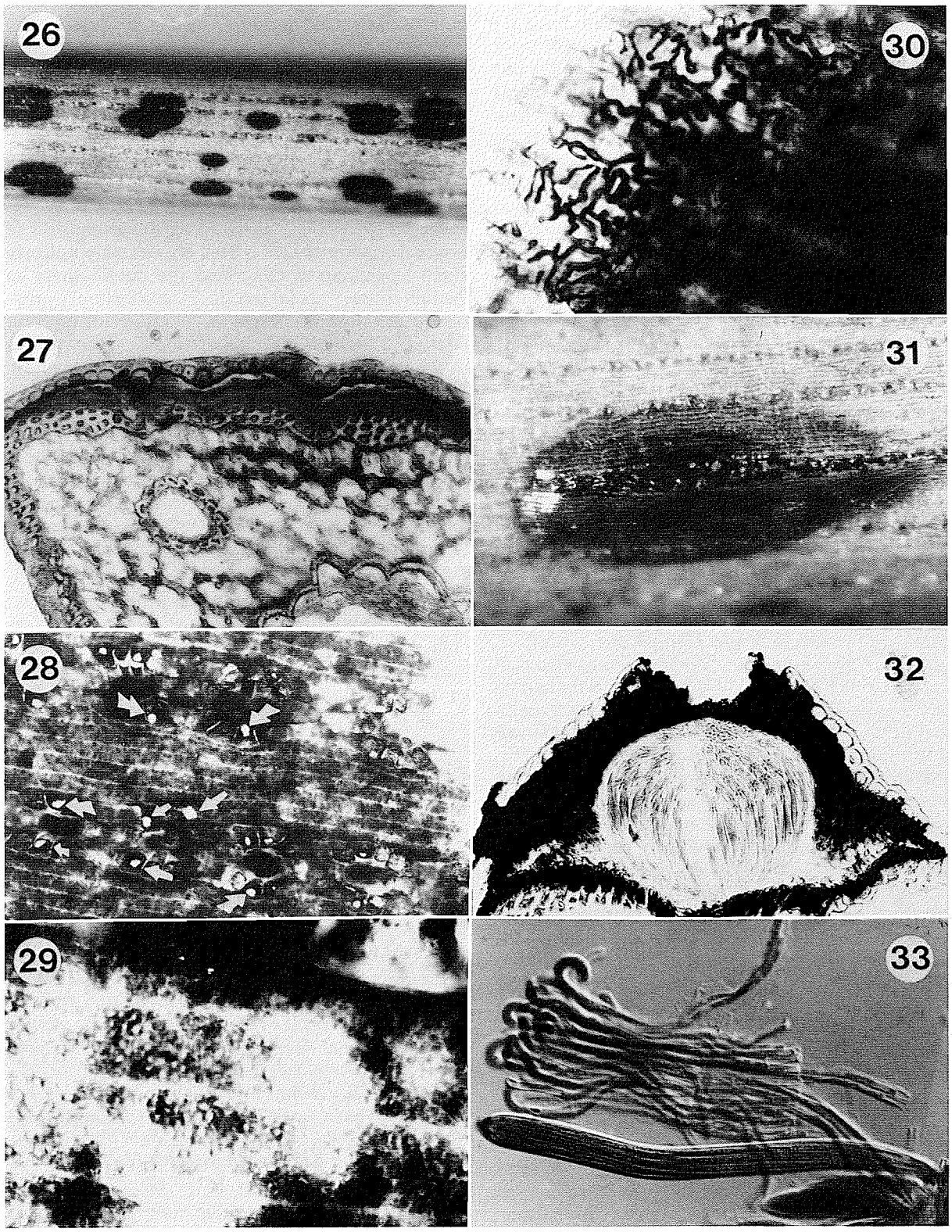
Lophodermium baculiferum Mayr, Die Waldungen von Nordamerika, p. 313 (1890) (Figs. 31–33)

Ascocarps amphigenous, dark grey or black, elliptical, 600–1200 µm long, totally covered by the needle epidermis, when mature opening with a single longitudinal split to expose the disc. The split characteristically occurs down a line of stomata and is not lined with lip cells. Paraphyses filiform, simple, septate, hooked at the tips. Asci cylindrical, eight spored, slightly rostrate, 90–170 µm × 10–15 µm. Ascospores filiform, aseptate, hyaline, smooth, fasciculately arranged and sometimes coiled within the ascus, 90–130 µm × 1.5–2 µm, enveloped in a gelatinous sheath 1–2 µm wide. Zone lines black, thin, infrequent.

NEOTYPE: On *P. jeffreyi*, Lassen National Forest, Lassen County, California, U.S.A., 15 August 1965, Lee Bonar (as *Lophodermium pinastri*), California Fungi 1273, IMI 142151.

Lophodermium baculiferum was described by Mayr from material (now lost, see Darker (1967)) on young pines of the *taeda* group (*P. ponderosa* and close relatives). According to the brief diagnosis, it differed from *Lophodermium pinastri* in having ascospores coiled within the ascus and paraphyses tips curved like the tops of walking sticks, hence the specific epithet (*baculus* Latin = walking stick). A small illustration of asci and paraphyses accompanied the diagnosis, with the magnification illustrated. The size of the asci and paraphyses as illustrated are consistent with the description above. Although Darker (1967) considered the name to be a *nomen nudum* probably synonymous with *Lophodermium pinastri*, it can-

FIGS. 26–30. *Leptostroma decipiens*. Fig. 26. Conidioma surface view. × 20. Fig. 27. Conidioma vertical section. × 170. Fig. 28. Conidioma surface view under transmitted light. Detail of ostioles occurring around stomata (arrowed). × 250. Fig. 29. As Fig. 28, but detail of upper wall texture. × 800. Fig. 30. As Fig. 28, but detail of upper wall edge aliform tissue. × 800. FIGS. 31–33. *Lophodermium baculiferum*. Fig. 31. Ascocarp surface view, note split along line of stomata. × 40. Fig. 32. Ascocarp vertical section. × 140. Fig. 33. Asci and septate paraphyses with characteristic curved apices. × 400.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not be so in view of this diagnosis and illustration. Although most species of *Lophodermium* have ascospores coiled in the ascus and many have more or less bent paraphyses, the specimen cited above has paraphyses with the tops so curved that it seems reasonable to revive the old epithet *baculiferum* for this taxon. *Lophodermium baculiferum* as neotypified above differs in opening along a line of stomata from all other described pine needle inhabiting species of *Lophodermium* which open between two rows of the epidermal cells which run between two lines of stomata. No other *Lophodermium* is totally subepidermal, lacks lips, and is associated with thin black zone lines running across the needle.

Discussion

The generic limits proposed above for *Leptostroma* agree in most respects with those given by Sutton (1980) though with some differences in the structure of the conidioma. His description, based on *Leptostroma scirpinum* Fr., a graminicolous species with a perfect stage in *Hypoderma* D.C., limited the genus to subcuticular conidiomata having an upper wall of textura angularis or prismatica, without ostioles, whereas in this study subepidermal conidiomata with aliform mycelium in the upper wall and with ostioles are included. There appear to be no species of *Hypoderma* with *Leptostroma* stages known on needles of pine, so direct comparison of Sutton's description with that given here is impossible. Darker (1967) however considered *Lophodermium*, *Meloderma*, and *Hypoderma* to form a complex of very closely related genera, and since within *Lophodermium* the *Leptostroma* stage can be subcuticular or subepidermal, with or without aliform tissue in the upper wall, and ostiolate or not, erection of a new form genus on these characteristics is not justified.

Although no true *Leptostroma* stages have been described on pine needles other than for the *Lophodermium* complex of genera, similar conidiomata are produced by other members of the Hypodermataceae, notably the *Lophodermella* Höhn. complex of genera (Darker 1967). These are excluded from *Leptostroma* in this treatment because although the conidia are similar in shape, size, and ontogeny, the conidiomata lack an upper wall (Uecker and Staley 1973).

Staley (1975) considered *Lophodermium nitens* and related taxa to belong to a separate subgenus from the bulk of pine needle inhabiting *Lophodermium* species on account of the different centrum ontogeny of the ascocarps. Their anamorphs (group 1) would tend to confirm this separation. Interestingly *Meloderma* has conidiomata morphologically close to the *L. nitens* subgenus. The groups of *Leptostroma* recognised here could provide a useful basis for dividing up the large and variable genus *Lophodermium*.

Doubtful or excluded species

Leptostroma pinastri Desm., Ann. Sci. Nat. II, 19: 338 (1843)

Most authors since Diedicke (1913) have regarded *Leptostroma pinastri* as the anamorph of *Lophodermium pinastri*. This is extremely unlikely since Desmazieres described the conidiomata as "epiphyllum, rotundatum, convexum, umbonatum, nitidum, nigrum, demum totum secedens," which may be rendered as "on the surface of the leaf, rounded, convex, shield shaped, shiny, black, eventually falling away completely," none of which bears much resemblance to the anamorph of *Lophodermium pinastri*. Although no specimen was listed in the original description, a collection from Desmazieres' herbarium has been examined and was found to contain numerous conidiomata of *Sirothyriella pini-austriacae* (Roum. & Fautr.) Sutton, a fungus which fits the original description perfectly.

Leptostroma hedgecockii Dearn., Mycologia, 20: 240 (1928)

Dearness described the conidia of this species as "snowshoe shaped, hyaline, with one large nucleus or two smaller ones in the wider (upper) end, 16–24 μ long by 4–6½ μ wide in the upper half, contracting to 2–3 μ at the lower end." A specimen identified by Dearness as this species (IMI 39561) has spores fitting this description. The conidioma is subhypodermal and has an upper wall more than one cell thick. This fungus, clearly not a *Leptostroma*, has doubtful affinities; it seems unlikely to be, as Dearness supposed, the anamorph of *Ploioderma hedgecockii* Dearn.

Leptostroma ahmadii Petr. In Petr. and Ahmad, Sydowia Ann. Mycol. 8: 181 (1954)

Examination of isotype material (IMI 94187) revealed long thin black conidiomata up to 6 cm long on the abaxial surfaces of needles, agreeing closely with the original description by Petrak and Ahmad. This appears to be the anamorph of *Bifusella linearis* (Peck) Höhn. and as such has the earlier name (see Darker (1967)) of *Hypodermium effusum* Schw.

Acknowledgements

The curators of BR, C, K, L, PC, and PAD are thanked for their assistance and permission to examine specimens in their care. Dr. B. C. Sutton is

thanked warmly for his advice and comments on the manuscript, and the assistance of Mr. D. W. Fry is gratefully acknowledged.

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